6

Causes of Decline and Strategies for Recovery of Klamath Basin Suckers

When the Lost River and shortnose suckers were listed under the Endangered Species Act (ESA), the U.S. Fish and Wildlife Service (USFWS) and others identified numerous factors that could explain their decline and their failure to recover after elimination of the sucker fishery (Chapter 5, Scoppettone and Vinyard 1991). Since the listing, many of these factors have been studied. As a result, understanding of the biology of Klamath suckers and of requirements for their recovery has improved. Information on suckers is found in over 500 articles, reports, memoranda, and critiques, although most are unpublished and so have not benefited from scientific peer review. The number of persons working on the suckers has grown from a few ichthyologists to several dozen scientists, resource managers, policy developers, consultants, and informed citizens. New information derived from the increased pace of documentation and research supports increasingly firm judgments on the current status of the species, probable causes of their decline, priorities for further study, and actions that should and can be taken to move the species toward the ultimate goal of recovery, as described in this chapter.

CRITERIA FOR JUDGING STATUS AND RECOVERY OF SUCKER POPULATIONS

Criteria for the assessment of status and recovery provide a useful point of departure for the causal analysis of decline of the endangered suckers and for evaluating proposals for their restoration. Criteria presented here are intended as a tool of convenience for present purposes; other criteria might be useful for other purposes.

Because each life-history stage of a population is linked to all other stages, unusual suppression of any life-history stage may be reflected ultimately in the suppression of the population as a whole. Thus, trends in the abundance of any stage can be chosen arbitrarily as an index of the status of a population. For the endangered suckers, the most convenient life stage to use as an index of status is the adult. As explained in Chapter 5, other stages are difficult to observe or sample, especially in large lakes, although attempts to do so are essential to the diagnosis of mechanisms that affect specific life-history stages.

If adults are used as an index of the status of the populations, three criteria, taken together, would indicate recovery: diversity in the age distribution of adults, annual entry of at least some individuals into the adult stage in most years from the younger life stages coupled with entry of large numbers of such recruits in some especially favorable years, and a population size that reflects carrying capacity for an environment that is generally well suited, although not necessarily optimal, for the suckers. The presence of multiple age classes of adults would indicate past recruitment to the adult stage and persistence of conditions suitable for the maintenance of adults. The combination of new recruitment in most years and very high recruitment in some years would indicate the general welfare of younger stages and successful spawning. The maintenance of populations at a density that approaches expected carrying capacity would indicate that growth and reproduction occur at sufficient rates to offset mortality through the life cycle as a whole.

As indicated in Chapter 5, the status of geographically defined subpopulations of the two endangered suckers varies drastically. Table 6-1 summarizes the status of various geographic subpopulations on the basis of the adults. As shown in Table 6-1, Clear Lake and Gerber Reservoir apparently support apparently stable subpopulations and therefore provide a basis for comparison with other subpopulations. The Upper Klamath Lake subpopulations, in contrast, do not meet the criteria for recovery, nor do they indicate recovery in progress. These subpopulations took an important positive turn after elimination of fishing in 1987, through the entry of new fish into the subadult and adult populations each year and through the production of one very strong year class (1991) and several moderately strong year classes during the decade of the 1990s (Chapter 5). Indications of no recovery without further environmental change, however, include the failure of adults to show an upward turn in overall abundances and the lack of a diversified age structure among older age classes, presumably because of repeated mass mortality of large fish.

Fishes of Tule Lake (and of the associated Lost River) show no signs whatsoever of recovery according to the criteria shown in Table 6-1. Lack of recruitment of young fish into the subadult and adult stages indicates lack of reproduction or negligible survival of young fish. Two additional locations, Lower Klamath Lake and Lake of the Woods, are listed even though they lack endangered suckers. These are locations where sucker populations conceivably could be established in the future. The mainstem reservoirs also are listed but belong to a somewhat different category because, as explained in Chapter 5 and further in this chapter, the potential for creation of suitable conditions for the entire life cycle is probably lower for these waters than for Upper Klamath Lake or the other waters where the suckers originally thrived.

REQUIREMENTS FOR PROTECTION AND RECOVERY

The ESA requires both protection and recovery of listed species (Chapter 9). Protection is accomplished by prohibitions of take and preservation of habitat. Protection alone is insufficient, however, in that the populations as a whole have shown a drastic decline over the last several decades, and there is no evidence that the populations are recovering.
At the subpopulation level, as indicated in Chapter 5, the balance between protection and remediation depends on location. Because the subpopulations of Clear Lake and Gerber

Table 6-1. Summary of Status of Geographic Subpopulations of Two Endangered Suckers in Upper Klamath Basin[a]

Geographic Subpopulations	Recovery Criteria[a] Age Structure	New Adults	Population Density	Required Actions	Priority[b]	Specific Actions
Clear Lake	+	+	+	Protection	1	Prevent alteration of tributaries; no drawdown exceeding 1992
Gerber Reservoir[c]	+	+	+	Protection	1	Same as for Clear Lake
Upper Klamath Lake	-	+	-	Remediation	1	Numerous, see Figure 6-1
Tule Lake	-	-	-	Remediation	2	Create spawning habitat[d]
Lake of the Woods	0	0	0	Remediation	2	Remove present fish; stock suckers
Lower Klamath Lake	0	0	0	Remediation	3	Raise level; stock adults[d]
Mainstem Reservoirs	-	-	-	Protection	3	Protect status quo or better

[a]According to Chapter 5 and three criteria described in text for evaluation of status and recovery.
[b]Priorities are based on the apparent ultimate value of subpopulation to recovery of population at large.
[c]Shortnose sucker only.
[d]Requires feasibility studies
Abbreviations: +, meets criterion; -, does not meet criterion; 0, population absent.

Reservoir are the only ones in the upper Klamath basin that meet the criteria for recovery as outlined above, their protection is of utmost importance for the long-term survival of the two endangered sucker species in the upper Klamath basin as a whole. These subpopulations appear to depend entirely on tributary spawning. Therefore, maintenance of tributary conditions suitable for spawning is an essential element of their protection. It is important that neither of the reservoirs be drawn down to extremes that would produce summer or winter mortality. Given the historical experience of the 1990s, the requirements of the 2002 biological opinion appear to be adequately protective in this respect, but it is critical for these subpopulations that no errors in judgment lead to extremes in drawdown beyond that observed in the 1990s.

The subpopulations of Upper Klamath Lake also have high priority but have different status. As explained in Chapter 5, they showed some encouraging responses to the curtailment of the snag fishery, but the numerical abundance of adults and the continuing attrition of old fish appears to be holding the population down and may even be driving it closer to extirpation. The pathway to recovery for this population is not clear. A great deal of the analysis of cause and effect in the remaining part of this chapter is devoted to the Upper Klamath Lake subpopulations because of their historical numerical importance and the lack of clarity about the means of achieving their recovery.

The Tule Lake subpopulations consist of a very small number of apparently healthy adults, but they fail to meet all three of the criteria outlined above for recovery: there is no evidence of recruitment into the adult stage, there is no diversification of age structure for adults, and abundances per unit area are low. Because the suckers are long-lived, the adults of the Tule Lake population are of high value, and also could be supplemented with salvaged individuals from other locations. The first step toward recovery of the Tule Lake subpopulations would be to establish spawning capability, which would require intensive work with tributary waters. Acquisition of water rights and steps toward the creation of (potentially artificial) physical habitat suitable for spawning and for larvae would be necessary initial steps toward recovery of these subpopulations. The Tule Lake subpopulations, although small, need not be written off as unrecoverable.

Listed fifth in Table 6-1 is Lake of the Woods. As explained in Chapter 5, this was the location of a population probably consisting of shortnose suckers, but the population was eliminated. The present fish populations of Lake of the Woods should be eliminated, and adult shortnose suckers and other native fishes should then be reintroduced. If the suckers meet the recovery criteria outlined above after a number of years, fish biologists could consider the reintroduction of game fish (fish other than suckers probably will have colonized the lake by that time in any event).

Lower Klamath Lake lacks suckers and is probably unsuitable for them (Chapters 3 and 5), but alteration of these conditions could be feasible. Steps should be taken toward acquisition of water rights suitable for maintenance of higher water levels in Lower Klamath Lake if feasibility studies support this approach. Adult suckers from salvage (as described later in this chapter) should then be transferred to Lower Klamath Lake. Water quality and habitat conditions may be unsuitable, but suitability can be determined most effectively by monitoring of trial reintroductions. To the extent that maintenance of higher water levels would interfere with agricultural use of land, its establishment would require negotiations and compensation for acquisition of private rights.

The last subpopulations mentioned in Table 6-1 are the ones in mainstem reservoirs. These reservoirs have value primarily for long-term storage of large suckers. They do not have high priority for recovery, because they are not part of the original habitat complex of the suckers and probably are inherently unsuitable for completion of life cycles by the suckers. Maintenance of adults in these locations does, however, provide some insurance against loss of other subpopulations.

Construction of fish ladders for suckers at the dams might facilitate return of fish from mainstem reservoirs to Upper Klamath Lake. A fish ladder at Link River Dam, which is scheduled for completion in January 2006, should receive high priority; movements of fish through the ladder should be monitored.

SUPPRESSION OF ENDANGERED SUCKERS IN UPPER KLAMATH LAKE: CAUSAL ANALYSIS AND REMEDIES

For several reasons, causal analysis of the suppression of endangered suckers deserves more attention for the Upper Klamath Lake subpopulations than for other subpopulations. First, despite severe suppression of endangered suckers in Upper Klamath Lake, these subpopulations still contain many fish. Second, the subpopulations in Upper Klamath Lake were large as recently as 50 yr ago, so it seems reasonable, lacking evidence to the contrary, that they could be restored by a reversal of one or more critical human-induced impairments that have occurred over the last 50 yr. Third, water management involving Upper Klamath Lake is the responsibility of the federal government through the U.S. Bureau of Reclamation (USBR), which has access to substantial resources and also has legal responsibility for reversing or moderating any adverse effects of its management of Upper Klamath Lake if causal linkages between management and harm to the suckers can be established. Fourth, even though the subpopulations of endangered suckers are suppressed in Upper Klamath Lake, all life stages are present and some recruitment appears to be occurring from one life stage to another every year; recovery seems feasible if some key factors can be identified and changed.

Actual or potential cause-and-effect relationships that explain the status of a population are hierarchical. For present purposes, *immediate* causes can be explained in terms of suppression of one or more stages of the life cycle. For example, suppression of the entire population could be explained entirely or in part by exceptionally high mortality of larvae. Suppression of more than one component of a population could prevent it from recovering. There can be more than one immediate cause of suppression of a population.

Proximate causes are environmental factors. An example is poor water quality that leads to mass mortality of adult fish. A single proximate cause may be linked to more than one immediate cause. For example, poor water quality may suppress not only adults but also other life-history stages.

Ultimate causes, in the present context, are direct or indirect results of human actions. For example, operation of unscreened canals is an ultimate cause of mortality of fish in various life stages. Human actions that have led to changes in the water quality of Upper Klamath Lake are ultimate causes of mass mortality of large fish.

Recovery of the populations of endangered suckers can be approached most efficiently through analysis of the three levels of causation that explain failure of the fish to recover. Because the possible combinations of cause and effect are numerous, remedial actions, which are expensive, must focus on chains of cause and effect that are most likely to produce recovery. Winnowing the importance of cause-and-effect relationships requires information, some of which must be quantitative to be useful. The task of the researcher or the monitoring team is to produce information, typically over a period of years, that can be used to support estimates of the suppression of the population by chains of causation involving specific life-history stages (immediate causes), specific environmental factors (proximate causes), and specific human actions (ultimate causes). Knowledge of causation can produce estimates of the beneficial effect of remediating the effects of human actions.

Intensive research on the endangered suckers has been under way for a relatively short time, especially in view of the complicating effects of natural variation caused by climate and other factors that are not under human control. Only a few causal relationships are known well enough to support remedial action with confidence, but some of these are among the most important because they explain notable mortality of one or more stages of the population. Eventually, some of the more subtle but still important types of impairment and their causes must be clarified, as indicated in the following overview and analysis of cause and effect.

The analysis of causal connectivity is summarized in Figure 6-1. The figure shows the life stages of the endangered suckers as presented in Chapter 5 and identifies potential proximate causes of suppression of each life stage. Because the life stages are interconnected developmentally, the underlying premises of the diagram are that suppression of any life stage contributes at least potentially to suppression of the overall population and that a potential remedy for the suppression of the population lies in the identification and reversal of the suppression of individual life stages. It is not a foregone conclusion, however, that reversal of a particular type of suppression on a specific life stage will move a population notably toward recovery.

Figure 6-1 shows connections between immediate, proximate, and ultimate causes as solid or dashed lines. Solid lines indicate causal connections that are well established scientifically; typically these connections involve phenomena that are easily observed or documented (such as mass mortality of adults or death due to entrainment). Dashed lines indicate causal connections that are under study and for which there is insufficient evidence to show them as unimportant, moderately important, or important.

The figure shows convergence of multiple lines on individual immediate causes in some cases. Thus, the diagram indicates the likelihood that some immediate causes of decline are explained by multiple factors and that the factors might interact in their effects on a specific life-history stage. In addition, the diagram indicates that some environmental factors (proximate causes) have multiple connections with immediate causes; that is, they can affect more than one life stage. This is also expected from the literature on fish populations. The last column in the diagram lists remedial measures; the degree of certainty in their effectiveness is discussed below. Even though the life-history stages are interdependent and so must be considered together in the final prescriptions for recovery, it is useful to consider them individually first because each stage is affected by a distinctive suite of environmental factors. The discussion therefore follows the life-history sequence.

Production and Viability of Eggs

The production of eggs is usually discussed in terms of spawning fish, which are much more easily observed than eggs. The eggs themselves are the concern, however, and successful spawning is only one element of their final value to the population. Low viability of eggs, for example, could undermine the effectiveness of successful spawning. No researchers have attempted to make a case that the viability of eggs differs in Upper Klamath Lake or its tributaries from what would be expected in an unimpaired environment. Thus, the present discussion focuses on spawning, but it should be noted that lack of discussion of the fate of eggs after spawning is due partly to lack of information.

Dams

Small dams are found in the tributaries of Upper Klamath Lake. Where it can be shown that the dams do not allow passage of fish attempting to spawn, they should be removed or, if a dam must be retained, it should be fitted with a functional bypass.

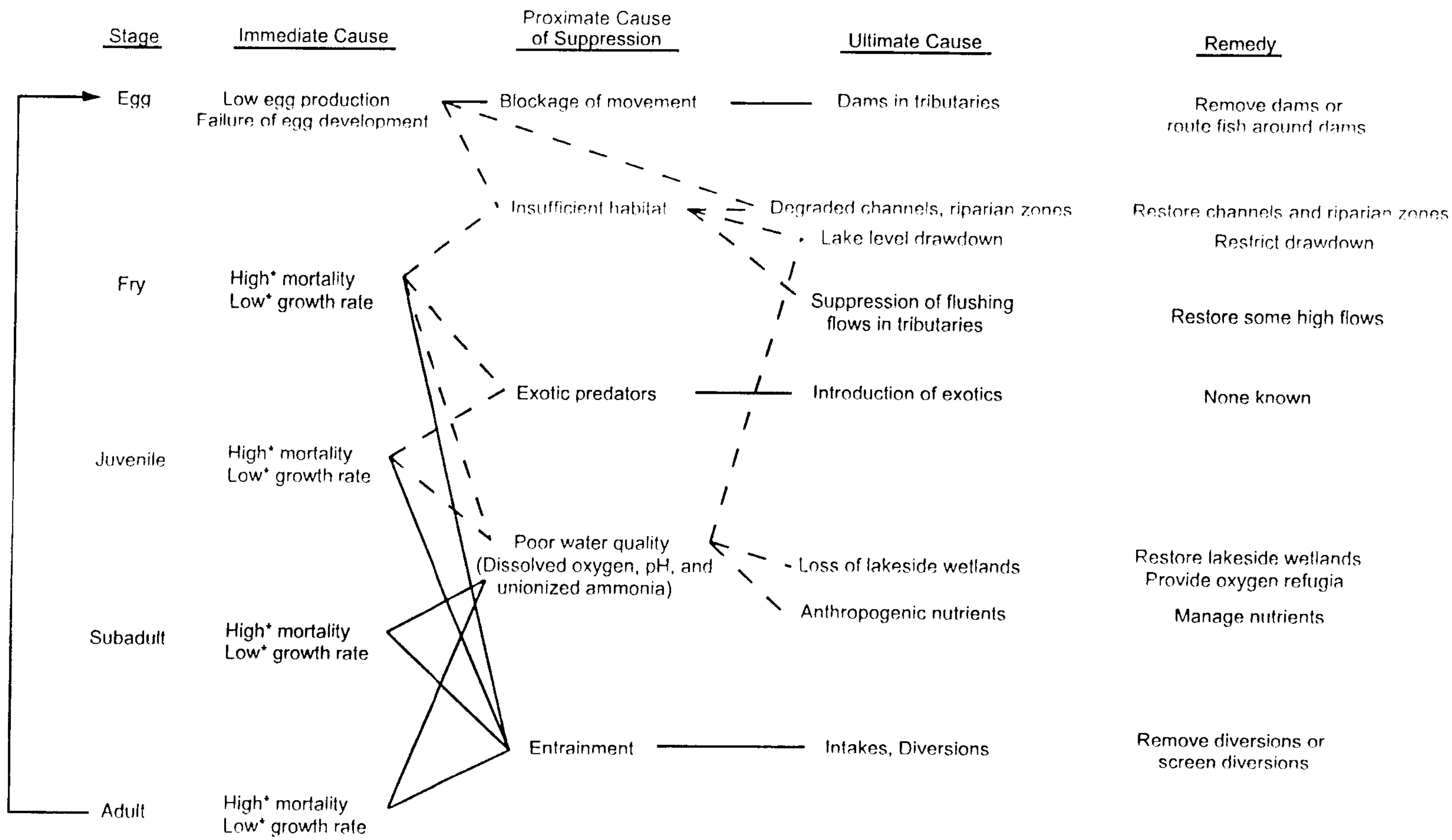

Figure 6-1. Diagram of causal connections in suppression of populations of endangered suckers in Upper Klamath Lake. Solid line = connection verified scientifically; dashed line = connection under study. "High mortality" and "low growth rate" are relative to rates in stable populations.

The only moderately large dam on a tributary to Upper Klamath Lake is Chiloquin Dam, which blocks the Sprague River near its confluence with the Williamson River (Figure 1-3). Construction of Chiloquin Dam in the early 1900s (1918-1924—the exact date is unclear) may have eliminated more than 95% of the historical spawning habitat in the Sprague River (53 Fed. Reg. 61744 [1988], p. 5). This possibility is based on total river miles above the dam and does not take into account unusable portions of the river or the ascent of the dam by at least a few spawning fish via the fish ladder each year. There are more fish below than above the dam, however, and few fish enter the fish ladder (e.g., Janney et al. 2002), although the actual number is unknown. Improved access to the upper Sprague River would increase the extent of spawning habitat and expand the range of times and the conditions under which larvae enter Upper Klamath Lake.

Proposals for improving access of suckers to spawning grounds on the upper Sprague River involve two possibilities: removal of the dam and improved fish passage at the dam. Scoppettone and Vinyard (1991) recommended removal of the dam, as have others since then (e.g., Klamath Water Users Association 2001). Stern (1990) estimated the cost of removing the dam at about $500,000 and of fish passage improvements at $560,000. CH2M HILL (1996) presented detailed plans for improvement of passage and estimated the cost at $1.445 million but gave no estimate for removal of the dam. The plan of CH2M HILL includes construction of a new vertical-slot ladder on the left bank (looking upstream) that would replace the present ladder, which is ineffective. The new ladder would be based on fish passage structures through which cui-ui (*Chasmistes cujus*) move up the Truckee River and into Pyramid Lake.

CH2M HILL (1996, p.2) dismissed removal of Chiloquin Dam because of "too many environmental concerns . . . as well as a lack of local support." The environmental concerns were not enumerated; presumably they are related to release of sediment and the difficulty of predicting how fish would respond to the new hydraulic conditions (e.g., Stern 1990). Issues related to sediments arise with virtually any dam-removal project, but often they can be resolved (Heinz Center 2002). The response of the fish is unknown, but removal of the dam is likely to result in a natural migratory response, at least by young spawners that have not already developed the habit of spawning downstream of the dam.

Lack of local support for removal of Chiloquin Dam is explained in part by water delivery via the dam to the Modoc Point Irrigation District (MPID). MPID involves about 60 farms and irrigates 3000-5300 acres annually, or less than 3% of the irrigable acreage in the basin. The MPID apparently has "adopted a Resolution indicating its willingness to participate in a project to restore fish passage" (Klamath Water Users Association, undated memo, about 2001) and is willing to consider moving its point of diversion away from Chiloquin Dam (E. Bartell, The Resource Conservancy, Inc., Fort Klamath, Oregon, unpublished report, 2002). Cooperation with MPID is important to the removal of Chiloquin Dam.

Removal of Chiloquin Dam has high priority and should be pursued aggressively. In the interim, spawning fish could be captured at the base of the fish ladder and released immediately above it; some of the released fish should be fitted with transmitters. Such a program would immediately give more fish access to the Sprague River and would show what upstream areas are favored by the fish. Continued monitoring below the dam also would provide information on numbers of adults returning downstream and numbers of larval fish reaching the lake. A summer sampling program could determine whether juveniles are in the river and would demonstrate the status of other native fishes in the river.

Water Level in Upper Klamath Lake

Spawning occurs at shoreline sites around Upper Klamath Lake from late February to May; maximum spawning activity occurs in March and April. More than 60% of spawning occurs in water more than 2 ft deep at locations with inflowing stream water (e.g., Reiser et al. 2001; see also Chapter 5). Inundation to a depth of at least 2 ft may be necessary for successful use of spawning substrate. At Sucker and Ouxy springs, two of the most frequently used sites (Hayes et al. 2002), lake elevations below 4142.5 ft place 55% and 67%, respectively, of the spawning area in water shallower than 2 ft. Reiser et al. (2001, p.7-2), in a separate analysis, concluded that lake elevations below 4142.0 ft "severely diminish available spawning habitat"; they recommend that Upper Klamath Lake be kept at full pool elevation (4143.3 ft) from mid-March to as late as mid-May to provide adequate water depth for spawning. Under recent operating regimes, water levels have remained above 4143 ft for extended intervals in wet years but have fallen well below 4143 ft in dry years (Figure 6-2).

Figure 6-2 shows the effect of water-level regulation in Upper Klamath Lake on spawning area according to the criteria proposed by Reiser et al. (2001). Under natural conditions, spring water levels would have been at or near full pool (4143.3 ft). Under conditions prevailing in 1990-2001, full pool elevation was achieved during the spawning interval in 6 of 10 yr; in the other 4 yr the water level was slightly lower to much lower, with corresponding consequences for the inundation of spawning sites.

It seems clear that drawdown of Upper Klamath Lake decreases the area of lakeside spawning habitat for the endangered suckers. Thus, a reasonable hypothesis is that lake levels below 4143 ft, and especially those below 4142 ft, suppress the production of larvae by reducing production of viable eggs, thus potentially affecting the population. In the absence of scientific information on the recruitment of larvae or other stages in years showing various amounts of water-level drawdown, professional judgment would be the only recourse for assigning significance of variations in spawning habitat to the relationship between production of larvae and water level in the lake. As a result of intensive study of the suckers, however, there is some direct evidence by which the hypothesis can be tested in a preliminary way.

Larval suckers have been sampled systematically since 1995 (Simon and Markle 2001). If drawdown suppresses spawning success substantially, one would expect lower relative abundance of larvae in years of extreme drawdown. The relationship between water level and abundance of larvae or juveniles would not necessarily be linear; it might involve thresholds rather than gradual changes in production of viable larvae.

Figure 6-3 shows the relationship between water level of Upper Klamath Lake in April (in the middle of the critical period) and relative abundances of larvae as shown by the standardized sampling program. Minor differences in relative abundances of larvae should not be considered significant because the sampling variance for any given year is substantial (95% confidence limits extend 50-100% around the mean in most cases). Thus, 1998 and 2000 might be considered distinctive in their scarcity of larvae, whereas 1995-1997 and 1999 belong to

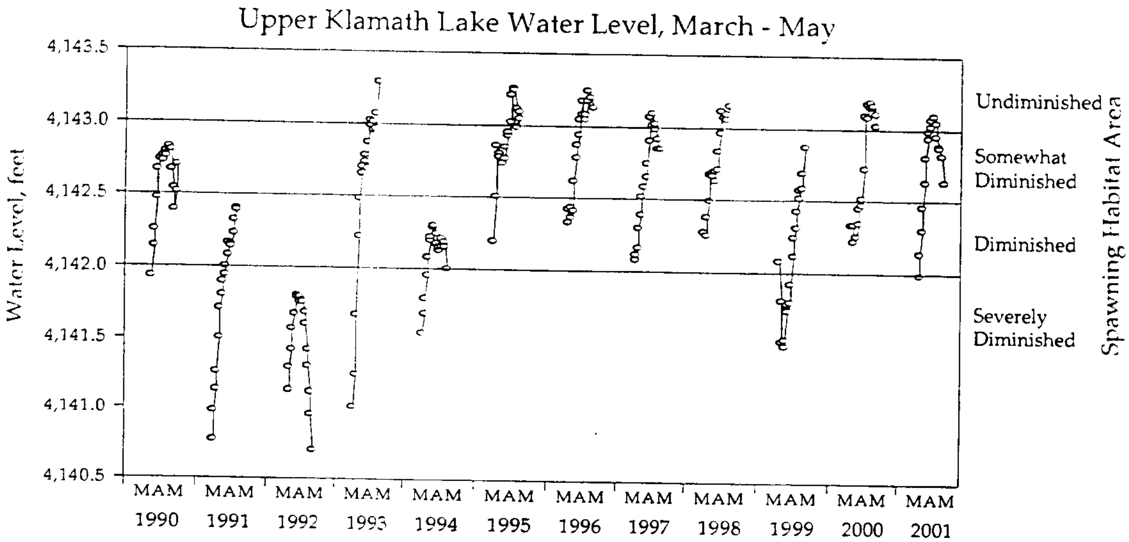

Figure 6-2. Water levels for 5-day intervals in Upper Klamath Lake over months of most vigorous spawning by suckers (March, April, and May—MAM), shown in context with spawning habitat designations given by Reiser et al. (2001).

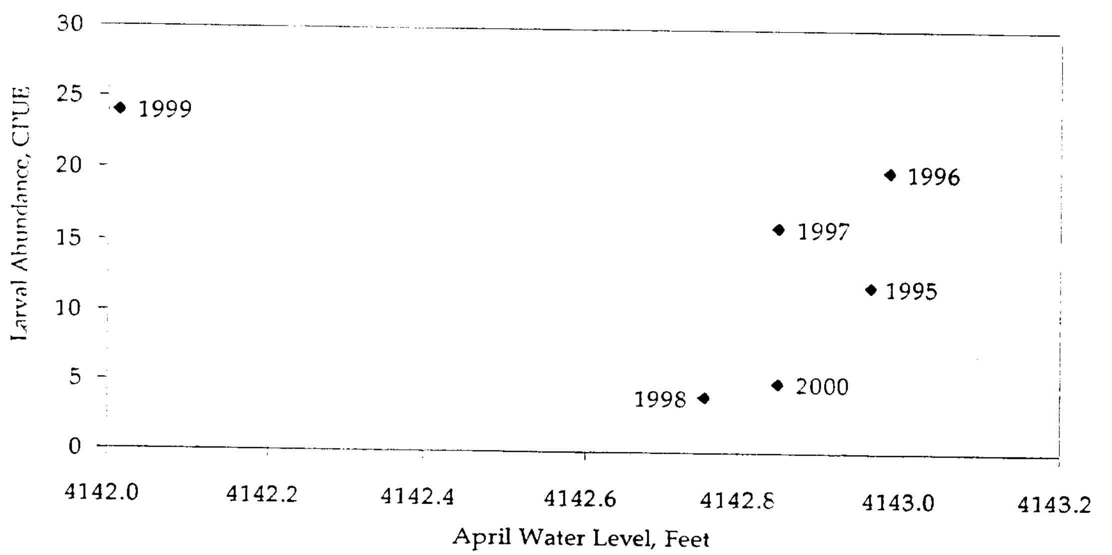

Figure 6-3. April water level and larval abundance (mean catch per unit effort [CPUE]) in Upper Klamath Lake. 95% confidence limits for annual means typically are 50-100% of the mean. Source: Simon and Markle 2001.

a second category of years involving much higher larval abundances that are virtually indistinguishable from each other because of sampling variance.

The year of lowest water levels during April was 1999, during which spawning habitat varied from somewhat diminished to severely diminished according to the criteria of Reiser et al. (2001; Figure 6-2). In all other years of the 6-yr record, the restriction of area was substantially less than in 1999. Thus, the hypothesis that diminution adversely affects production of larvae from eggs is contradicted by this test. The test is not particularly strong, because extremes of diminution and repeated years of diminution are not available in the record. Further observation might demonstrate some relationship that is not now evident. For the present there is no indication of a strong relationship between spawning success, as inferred from abundance of larvae, and water level in Upper Klamath Lake.

One other empirical test is possible. It is more remote in a life-history sense because it involves the relative abundance of adult fish. Its advantage is that it involves data that extend into different water years from those available for testing through larval abundance.
As explained in Chapter 5, mass mortality of fish provides insight into the age structure of the endangered sucker populations. Specifically, the relative abundance of age classes of subadult and adult fish can be judged on the basis of their relative frequency of appearance among fish that are collected after the fish kill. As indicated in Chapter 5, any use of this information must be considered provisional because the relationship between the actual age structure of the population and the age structure reflected in the fish kill is unknown.

Given the assumption that large fish are killed in relation to their abundance in the population, relative abundance of specific year classes of fish should reflect the developmental history of each year class. If repression of larval production through restriction of spawning areas is critical in years of low water level in the lake, years affected by low level should stand out as producing a reduced population of large fish, given that large fish are ultimately a byproduct of successful spawning. The relationship between lake level and relative abundance (percentage frequency) of fish is shown in Figure 6-4. As indicated in the figure, the 2 yr of extraordinarily low water levels (1992 and 1994), which would be expected to show most strongly the negative signal involving larval production, do not indicate any repression of the year classes related to water level.

Further research may show a relationship between inundation of the spawning area and larval recruitment. Present data suggest, however, that any such relationship would be either weak or indirect. Thus, the connection does not appear to be especially important for the population. This conclusion seems counterintuitive, but there are several potential explanations. First, the present population, which is much smaller than the original population, may have adequate spawning area even when spawning area is reduced, simply because it puts less total demand on the spawning area. Thus, progressive recovery of the population could produce a bottleneck related to spawning area in the future. Second, recruitment from spawning in streams may be more important than lake spawning under present circumstances. These and other possibilities cannot be distinguished at present. Overall, maintaining full pool elevation for promotion of spawning, although intuitively appealing, is difficult to defend scientifically.

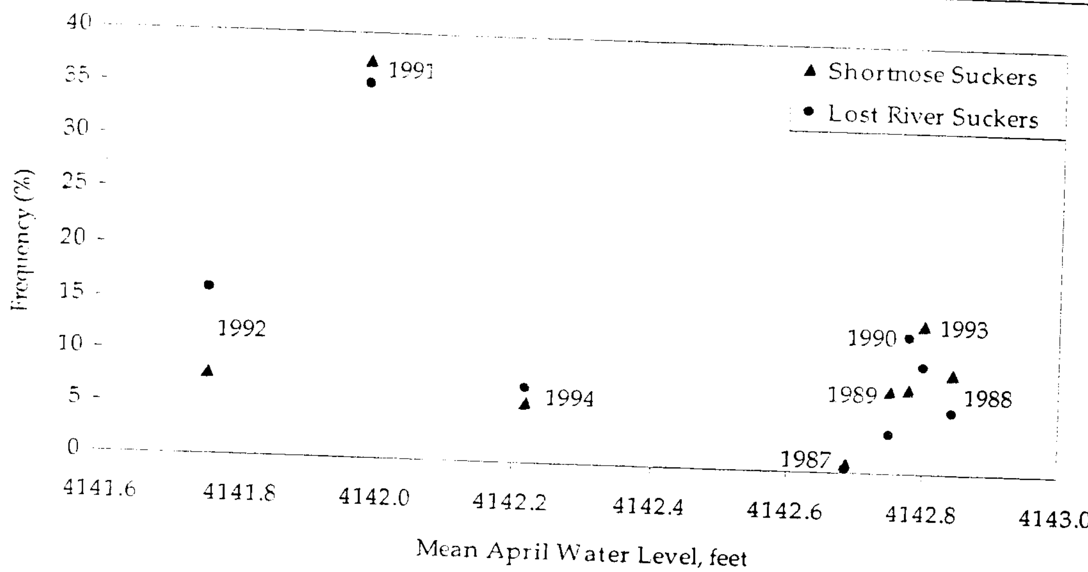

Figure 6-4. Relative abundance of year classes of suckers in Upper Klamath Lake, as inferred from fish recovered after mass mortality in 1997, in relation to water level during spawning interval when same year classes were produced. Source: USGS, unpublished data, 2001.

Degradation of Spawning Areas

Some lacustrine spawning areas appear to be degraded, as indicated in Chapter 5. Where feasible, degraded spawning areas should be restored by introduction of additional gravel in appropriate type and size, removal of silt, or redirection of spring flows. It is unclear whether these actions will increase sucker spawning success, but they are not especially expensive and may be beneficial. Potential diminution of depth must be taken into account if restoration involves the addition of new substrate. Also, factors other than depth per se need to studied more extensively with respect to the suitability of spawning areas. Wave action and other factors that have not yet been studied might be relevant, for example.

While lakeside spawning areas for suckers in Upper Klamath Lake have been studied extensively, tributary spawning areas have received relatively little attention. Where tributary spawning occurs, the morphometric features and substrate composition favoring the suckers should be identified, and specific efforts should be made to offset any changes in these characteristics that may have occurred through anthropogenic mechanisms. In addition, potential adverse effects of suspended load should be identified. Improvement of appropriate conditions for spawning will likely require protection of riparian zones from grazing and other disturbances, reduction in transport of suspended load related to land disturbance through agricultural and other land-use practices, and restoration of wetland near channels. Furthermore, it may be effective to protect specific spawning regions of tributaries from human presence in order to reduce the possibility of harassment and to increase public awareness of the importance of specific locations for successful spawning by suckers.

Some tributaries and lakeside spawning areas that are known to support successful spawning by suckers may not require restoration but do require vigorous protection because of their special value to the population. Even subtle changes, which might involve pumping of ground water in the vicinity of these spawning sites, land disturbance, recreational activities, poorly managed agricultural practices, and other human activities could easily degrade or even eliminate these sources of sucker fry.

Abandonment of Spawning Areas

Some historical spawning areas have been abandoned for no apparent physical reason. Reestablishment of population components with natal affinities to the areas should be attempted. The degree of benefit cannot be estimated from present information, but the work could be accomplished without great cost. Specific locations are as follows:

1. Harriman Springs in northern Upper Klamath Lake was last used in 1974; spawning was also reported historically at Odessa Creek on the western shore (Andreason 1975, USFWS 2002). Barkley Springs on the southeast shoreline of Upper Klamath Lake was a previous spawning site but has not been used since the late 1970s (Perkins et al. 2000a), because diking, ponding, and rerouting of water associated with the construction of Hagelstein Park in the 1960s apparently blocked access of the fish to the site. Spawning substrate was added and water-control devices designed to inundate the springs were constructed in 1995, but no spawning has yet been observed.
2. Spawning suckers were reported at a spring on Bare Island (in the northern portion of Upper Klamath Lake east of Eagle Ridge) in the early 1990s, but spawning has not been observed at the site since then (Perkins et al. 2000a).
3. In the region of Agency Lake, spawning of suckers was observed in the late 1980s and early 1990s in Crooked Creek, Fort Creek, Sevenmile Creek, Fourmile Creek, and Crystal Creek. The Wood River has had the only recent spawning activity, most of it attributed to shortnose suckers. Adults were last seen in the Wood River in 1996, and larvae were last collected in 1992; no juveniles were found in 2000 (Simon and Markle 1997b, 2001; Cooperman and Markle 2003).
4. Additional, indirect evidence of abandoned spawning sites in Upper Klamath Lake itself has been obtained on the basis of lost fishing gear (Cooperman and Markle 2003). Shoreline surveys conducted during record low lake levels in 1994 revealed fishing gear on the bottom at known spawning sites, such as Ouxy and Sucker Springs. Lost gear also was found at four unnamed, flowing spring sites between Modoc Point and Sucker Springs. Failure to observe suckers spawning at these four sites during recent spawning surveys suggests that direct removal or harassment led to the elimination of the spawning aggregations.

The available evidence strongly suggests that lake and stream spawners mix only occasionally if at all and that spawning-site fidelity causes an abandoned spawning site to remain unused. Abandonment of apparently appropriate spawning sites indicates that the use of a spawning site is a social tradition, that is, that fish learn about spawning sites by following or observing other fish (e.g., Helfman and Schultz 1984). A good spawning site may remain unused by fish that show those characteristics if "teachers" are absent, as has been demonstrated for reef-spawning wrasses in the Caribbean (Warner 1988, 1990). Use of abandoned sites might be renewed spontaneously if populations of adults become substantially more abundant.

The possibility that sites are abandoned because of a break in tradition suggests a solution. Transplantation of spawning-ready fish of both sexes to historically used sites, perhaps accompanied by confinement of the fish in cages for a brief acclimation period, might initiate use of the abandoned sites. Feasibility of this approach is suggested by Warner's (1988, 1990) manipulations, which involved transplantation of fish to locales that had been experimentally depopulated, with subsequent establishment of site-specific, traditional spawning groups by transplanted individuals. Males might be attracted to caged females in spawning-ready condition; spawning readiness could even be induced, if necessary, by hormone injection. Fish could be transplanted from habitats that lack recruitment—such as Tule Lake, the Lost River, or the Klamath mainstem reservoirs—assuming that spawning-ready individuals are available. If fish from Upper Klamath Lake are used for such manipulations, they should probably be young, first-time spawners because fish with spawning experience are likely to abandon a new site for a site with which they are familiar.

Regardless of the cause of spawning-site abandonment, loss of spawning aggregations has several consequences for sucker recovery. If the aggregations at these sites represented genetically distinct groups of suckers, overall genetic diversity of the Upper Klamath Lake populations probably has been reduced. Even without genetic distinctness, the uniqueness of circumstances at each site creates potential differences in survival of larvae originating at different sites. Multiple spawning sites have a bet-hedging effect on larval survival: the more spawning sites a population uses, the more resistant the population is to exceptional loss at any one site.

Survival of Larvae and Juveniles

Mortality of larval and juvenile stages of all fishes is high, even in populations that successfully saturate their environment. High mortality in the young stages of the life history of a given fish population does not necessarily indicate that these stages are a bottleneck that leads to repression of the population. Survival of larval and juvenile stages in a repressed population could be usefully compared with those in a vigorous population; a bottleneck at the larval and juvenile stages would be indicated by substantially lower survival rates in the repressed population than in the vigorous population. However, estimation of survival rates of young life-history stages of fish is extremely difficult, and less direct indicators often are the only recourse for assessment of these stages, as is the case for sucker populations of Upper Klamath Lake.

Morphological Anomalies in Young Fish

Morphological anomalies—which may indicate parasitism, dietary deficiencies, or physiological stress during development—suggest abnormal losses of young fish during development. Where fish are not under physiological stress due to poor water-quality conditions, morphological anomalies seldom exceed 1% (Karr et al. 1986). In Upper Klamath Lake, however, the frequencies of anomalies among the larval and juvenile shortnose suckers averaged 8%, and among the Lost River suckers averaged 16% (Plunkett and Snyder-Conn 2000). The anomalies included deformities of the fins, eyes, spinal column, vertebrae, and osteocranium, as shown by Plunkett and Snyder-Conn (2000), who suspected chemical agents of human origin. These authors reviewed literature indicating high frequencies of anomalies in other fishes as well (fathead minnows and chub species) and in amphibians of the Upper Klamath Lake basin. Harmful agents have not yet been identified.

Skeletal deformities in young fish can affect their swimming performance and indirectly increase their vulnerability to predation and impair their ability to escape unfavorable habitat conditions. Plunkett and Snyder-Conn (2000, p. 2) suggest that the relatively high rate of anomalies in young suckers could result in "early elimination of anomalous 0-aged suckers from Upper Klamath Lake populations." Direct comparisons with populations in Clear Lake and Gerber Reservoir, where populations are apparently stable, would be informative.

Entrainment of Larvae and Juveniles

Entrainment at and lack of passage through Klamath River dams and other irrigation structures were added to the list of threats to the endangered suckers after the original listing (e.g., USFWS 1992a). Entrainment into irrigation and power-diversion channels is now recognized as being responsible for loss of "millions of larvae, tens of thousands of juveniles, and hundreds to thousands of adult suckers each year" (USFWS 2002, Appendix C., p. 24). Sucker larvae appear at the south end of Upper Klamath Lake beginning in late April. Millions of young fish then are swept from Upper Klamath Lake into the Link River, whence large numbers are drawn into the A Canal (USFWS 2002), from which they cannot escape.

Speculation has developed about the source of the young fish that reach the Link River. They may come from known spawning sites along the northeastern portion of Upper Klamath Lake, from such tributary streams as the Williamson River, or from unknown spawning sites farther south. Because all known spawning sites are in the northern portions of the lake, the critical question is whether currents in the lake are strong enough and of proper alignment to deliver larvae to the Link River 18 mi to the south.

Some evidence indicates that larval and juvenile fish entering the Link River originate in known riverine and lake spawning areas. Prevailing winds are from the northwest when larvae are present and establish substantial south-flowing currents, according to a numerical model developed by Philip Williams & Associates (PWA 2001). The Philip Williams model suggests that it is very feasible for larvae produced from the Williamson and Sprague system to enter the south end of the lake within a few days of swimup, the time at which larvae first leave the substrate for the water column (R. S. Shively, U. S. Geological Survey, Klamath Falls, Oregon, personal communication, 2002). Whether entrainment is caused by natural movement of fish that would historically have entered Lower Klamath Lake or is an avoidance response to poor habitat or poor water-quality conditions is unknown. Regardless, given that these larvae likely originate in known spawning aggregations and that any larvae leaving the lake to the south are permanently lost from the population, entrainment of young fish is a potentially important contributor to failure of the populations to grow.

USBR was scheduled to place fish screens at the A Canal in the summer of 2003. These screens function effectively with fish larger than 30 mm (USWFS 2002). Although retention of fish smaller than 30 mm could be achieved, the likelihood that very young, fragile fish would survive impingement (along with algae and debris) on the screens is low, and the chances of salvaging them successfully are even lower. Juvenile fish may survive impingement but, unless they move against the current, will still be lost from source populations because fish screened from the A Canal will next pass through the Link River Dam and then enter other canals, be killed by turbines, or join nonreproducing populations downstream (Figures 1-2 and 1-4). Even so, the screening does prevent loss of subadults, adults, and some juveniles through the A Canal.

USFWS (2002) recommends coordination of intake at the A Canal with timing of juvenile movements, deflection barriers that would move juveniles away from intake structures, location of intakes above the water-column strata in which young suckers usually swim, and salvage. These measures seem reasonable and should be pursued. Salvage operations may be pointless, however, if emigration from the lake is an avoidance response to poor water quality. Salvaged fish possibly could be moved to a holding facility with good water quality before return to Upper Klamath Lake or could be transplanted to other sites to establish new populations.

Adequacy of Nursery Habitat for Larvae and Juveniles

Upper Klamath Lake has lost an estimated 66% of emergent marsh vegetation and submerged vegetation (USFWS 2002). Specific changes include the apparent loss of emergent vegetation in the region between the Williamson River mouth and Goose Bay that probably once was important larval habitat; vegetation should be restored in this area as soon as possible. In general, diking, draining, and water-level management have reduced emergent and submerged vegetation along shorelines by about 40,000 acres (USFWS 2002). Remaining marginal marshes around Upper Klamath Lake are reduced, patchy, and often dewatered by middle to late summer as water level falls.

Vegetation in shallow water is a consistent aspect of larval habitat and may be important to juvenile habitat as well (Chapter 5). Abundance of this habitat feature during the larval phase, which extends from April through July, in Upper Klamath Lake is in part related to water depth. Higher water levels in Upper Klamath Lake are associated with larger amounts of emergent vegetation (Table 6-2). Ignoring emergent vegetation, total shoreline area that is at least 1 ft deep at lake water levels of 4142-4143 ft accounts for at least 50% of the lake's perimeter, but this fraction declines rapidly with reduced water levels. Very little emergent vegetation is available to larval suckers below a lake level of 4141 ft; emergent vegetation is essentially inaccessible below 4140 ft (Reiser et al. 2001). Reiser et al. (2001) recommend maintaining water levels above 4142 ft at least until July 15 to ensure access by larvae and juveniles, although the data on use of this habitat by juveniles are not clear.

Because the majority of suckers in Upper Klamath Lake now spawn in the Williamson and Sprague river system, use of habitat in the system by larvae could be important in determining production of larvae. Under current conditions (blockage of spawning migrations at

Table 6-2. Estimates of Larval Habitat Availability Calculated as Percentage of Lakeshore Inundated to a Depth of at Least 1 Ft for Lake Edge and Marsh Regions in Northeastern Upper Klamath Lake that Contain Emergent Vegetation, and Total Lake Shoreline Regardless of Vegetation

	% Larval Habitat Available			% Lake Shoreline Available
Water Level, Lake (ft)	Dunsmoor et al. 2000	Reiser et al 2001	Chapin 1997	Reiser et al. 2001 (All Shoreline)
4143.0	-	-	-	85-100
4142.8	80[a]	-	-	-
4142.0	50[a]	100[b]	-	40-60
4141.5	-	80[b]	-	-
4141.2	-	80[c]	-	-
4141.0	-	-	-	10-25
4140.0	0[d]	0	0	-

[a]Shoreline emergent vegetation.
[b]All emergent vegetation.
[c]Marsh edge habitat only.
[d]Almost completely unavailable.

Chiloquin Dam combined with a highly modified stream channel in the lower Williamson delta), a higher proportion of larvae may be produced in the lower Williamson than were produced there historically. As a result, the larvae may pass from the river to the lake more quickly and with less temporal dispersion than was the historical norm. Cooperman and Markle (2000) found that larvae left the Williamson River in as little as a single day and that 99% of larvae entering the lake had not yet developed a tail fin and so were not yet competent swimmers and feeders. The majority of larvae in the lower river sampled by Cooperman and Markle (2000) had empty guts. Thus, many larvae may be entering Upper Klamath Lake before they are ready to feed or to avoid predators (comparisons with Clear Lake and Gerber Reservoir populations would be useful but are not available). Modifications to the lower Williamson have reduced plant cover, and thus possibly reduced food production and shelter from predators. The Nature Conservancy is restoring the lower Williamson to a more natural, meandering, multiple-channel configuration that supports denser riparian and emergent vegetation. This project should be completed soon. Larvae descending from the Williamson system will find cover near the mouth of the river when vegetation and morphology have begun to recover, which may take some time.

Physical conditions that may impair spawning and support of fry in the rivers above Upper Klamath Lake have not been adequately studied. Changes in river channels have occurred as a result of removal of riparian vegetation, access of cattle to the streams, alteration of flows, and loading of the stream with fines. All of these factors should be documented and measures should be taken to reverse them on grounds that these changes are quite likely to interfere with successful spawning and larval survival.

Hypotheses about the significance of lake-level changes and capacity of Upper Klamath Lake to sustain larval suckers can be tested against information on the relative abundance of sucker larvae, as determined over the years 1995-2000. If interannual variation in lake levels is a dominant factor in the viability of larvae in the lake, years of higher lake level during the larval development period should be marked by higher larval abundance. To be of use in management, any beneficial effects of high water level should appear as higher CPUE (catch per unit effort) of larvae. This is not the case, however (Figure 6-5). In fact, the amount of larval habitat in spring varies across years much less (about 2-fold; compare Figure 6-5 with Table 6-2) than larval abundance per unit area (as indicated by CPUE—10-fold).

Additional testing is possible through use of information on relative abundance of year classes among fishes collected during episodes of mass mortality. If interannual variations in lake level correspond to relative degrees of repression of larval production, and this factor has a major effect on the populations, year classes produced in years of especially low water levels in Upper Klamath Lake should be exceptionally weak. Once again, this is not the case (Figure 6-6).

Lack of correspondence between larval abundance and indicators of year-class success based on either collection of larvae or collection of adults does not contradict the idea that inundated vegetation is critical habitat, that is, habitat that the suckers need in some unknown amount and distribution. It does call into question the idea that greater or smaller abundance of this habitat feature from one year to the next is regulating the populations. Cooperman and Markle (2003) have argued that complicating factors could mask an important relationship between water level in Upper Klamath Lake and production of larvae. From a scientific viewpoint, however, the water-level hypothesis is not supported because it fails empirical tests for the presently available data. An argument for a complex relationship involving water level would require empirical support, of which there is none. One potential line of investigation would be to examine the differences in larval production of the two sucker species. The two species appear to be responding in similar ways to environmental change, but the data suggest that the responses are not exactly the same. Differences related to timing or place of spawning may be important.

From a management perspective, the difficulty with a water-level hypothesis that involves unknown complications is that observations of higher water levels at present offer no evidence that would support maintenance of higher water levels. At the same time, the lack of a relationship between observed water levels and larval abundances cannot be taken as justification for broader manipulation of water levels, which at some extreme could be notably harmful.

Monitoring of larval abundance and year-class abundances as inferred from mass mortality indicate that the explanation for interannual variability at present lies in key factors other than the amount of shallow water or emergent vegetation. This conclusion should energize the investigation of other habitat features. For example, restricted availability or poor condition of tributary spawning areas could be critical. Interannual variability of year-class abundance as affected by delivery of larvae from tributary spawning areas would be an obvious subject for further study.

The known biology of the suckers indicates that particular depths are preferred at established spawning locales and that flooded emergent vegetation is primary larval habitat. The lack of relationship between water level in Upper Klamath Lake and larval production or larval survival indicates that other factors, such as degraded water quality or poor larval habitat,

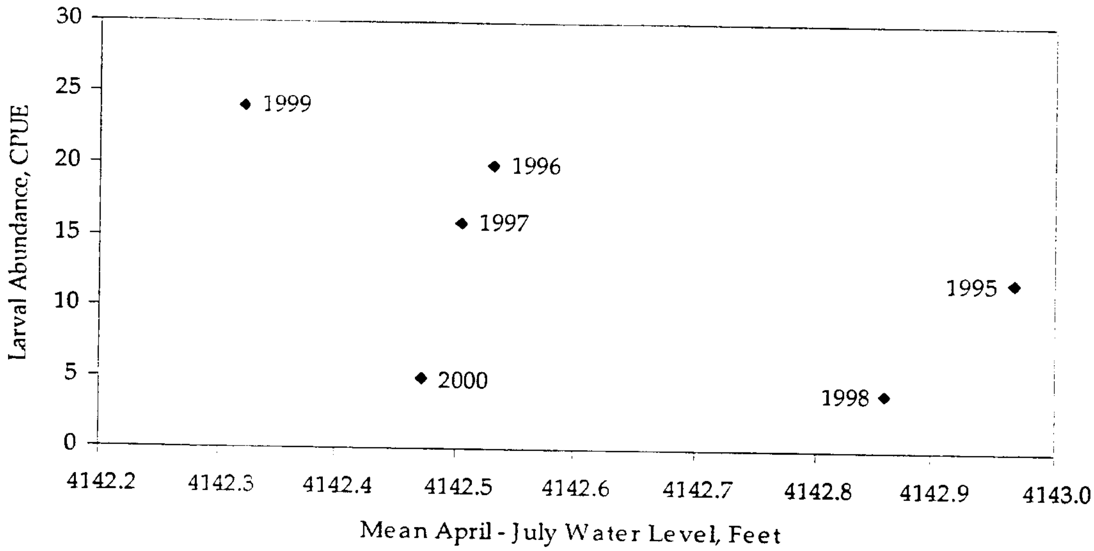

Figure 6-5. Relative abundance of larvae as determined by standardized sampling, shown in relation to mean water level of Upper Klamath Lake during the main interval of larval development (April-July). Source: Simon and Markle 2001.

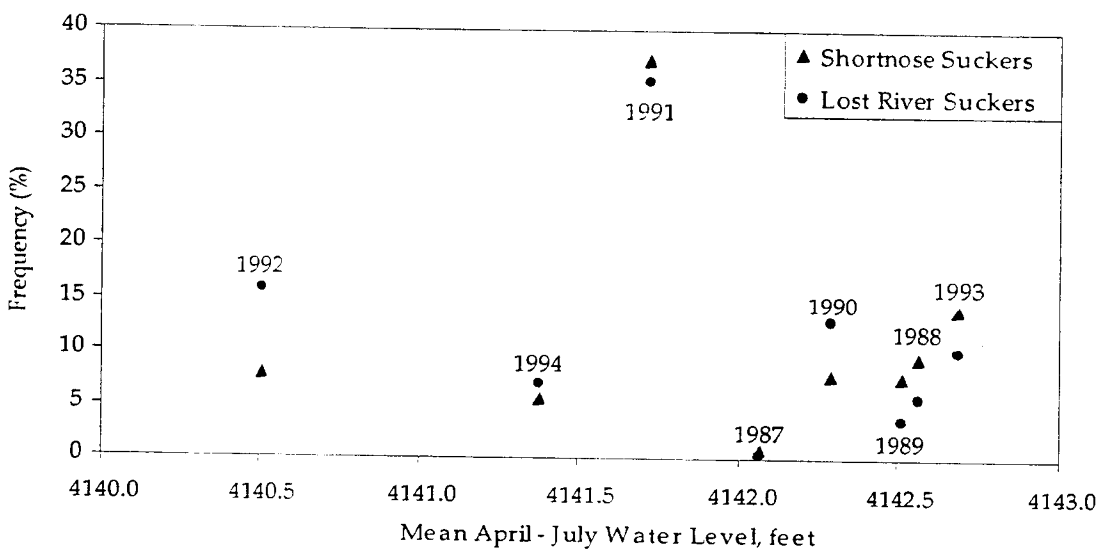

Figure 6-6. Relative abundances of year classes of endangered suckers collected from Upper Klamath Lake during the fish kill of 1997, shown in relation to mean water level over the interval of larval development for the same year classes. Source: USGS, unpublished data, 2001.

override the presumed benefits of depth-related habitat availability. Recommending maintenance of particular water levels to promote sucker recovery has no clear scientific basis until the factors that override water depth are better understood and, if possible, rectified. USFWS may retain an interest in water-level manipulations as justified by the need to minimize risk. Given limitations on the legitimate use of the need to minimize risk, however (Chapter 9), it might be difficult for USFWS to justify more stringent limitations on water level as a general operating rule. One alternative is for USFWS to work with USBR in testing various water-level combinations that can be achieved through such actions as experimental use of water-bank resources or by use of the excess water that may be available in some years.

Overview of Larval and Juvenile Production

As explained above, larvae were variably abundant in trawl catches throughout the 6-yr monitoring period 1995-2000. Catches were high in 1995, 1996, 1997, and 1999, and were relatively low in 1998 and 2000. No correlations are obvious between abundance of fish in spawning runs and larval abundance (Simon and Markle 2001, USFWS 2002) or between fish kills and larval abundance. Abundances of young of the year (YOY) also have high year-to-year variation and lack any detectable relationship with abundance of spawners. The year 1999 was good for larvae and juveniles regardless of sampling locale or method (Simon and Markle 2001, USFWS 2002), and 1991 must have been favorable as well, as judged from abundance of adults (monitoring of larvae did not begin until 1995).

As in most fish populations, abundance of young suckers in Upper Klamath Lake declines progressively through each summer and fall (Simon and Markle 2001). Declines could be explained by offshore movement as the fish grow, high mortality, high emigration rates from the lake, or a combination of these. Abundance of juveniles in spring (age 1+ yr) appear to reflect a 90% overwinter mortality or emigration (Simon and Markle 2001). High incidences of physical abnormalities in these fish (Plunkett and Snyder-Conn 2000) imply that mortality or export may repress recruitment of subadults and adults, although avoidance of sampling gear by postlarval fish creates difficulties in interpretation.

Some minimal number of spawners is necessary to produce a successful year class of larvae, but the lack of correlation between numbers of spawners and abundances of larvae implies that abundant spawners are no guarantee of high larval numbers and that, given the high fecundity of suckers, a small number of spawning fish may be sufficient to produce abundant larvae if conditions for larvae are good.

Adults

Entrainment

Fish that enter water-management structures typically cannot return to the habitat from which they came or enter another suitable habitat. For Upper Klamath Lake, the A Canal has long been recognized as a source of entrainment for all life-history stages, including adults, whose loss may be especially significant because of the importance of large fish in maintaining the fecundity of the population (Chapter 5). Scheduled screening of the A Canal, which will be ineffective for small fish < 30 mm, will block entrainment of subadult and adult fish, and could thus reverse an important historical source of mortality. The benefits of this measure to the population are unknown. Entrainment of fish from Upper Klamath Lake via the Link River still occurs through intake structures of the Link River Dam, which should be screened (USFWS 2002).

Mass Mortality

Unlike most other imperiled lakesuckers, suckers of Upper Klamath Lake suffer from episodic mass mortality of reproductive-age fish. Although such mortality probably inhibits recovery, fish kills are not new to Upper Klamath Lake. Records indicate periodic kills dating at least to the late 1800s; before the 1990s, large fish kills occurred in at least 1894, 1928, 1932, 1966, 1967, 1971, and 1986 (USFWS 2002). Whether episodic mass mortality has always occurred in Upper Klamath Lake is a matter of conjecture.

The actual numbers and sizes of fish killed are difficult to estimate because of sampling difficulties, differential sampling effort, loss of small fish to birds, and loss of fish that do not float after death. Mortality may reach tens of thousands in a severe episode (Perkins et al. 2000b). The effects of fish kills on spawning populations of suckers probably have been substantial. As much as 50% of the adult populations may have died in the 1996 fish kill; sizes of spawning runs indicate that the spawning populations of both species were reduced by 80-90% from 1995 to 1998 (USFWS 2002; Chapter 5).

The largest documented case of mass mortality occurred in 1971; it involved the loss of about 14 million fish, most of which were blue and tui chubs. Water level may or may not have played a role in conditions leading to the incident, but 1971 was the year of highest recorded water level since full operation of the Klamath Project began in 1960. It is unclear whether the extent or frequency of mortality is greater now than earlier. Incidents of mass mortality in 3 consecutive recent years (1995, 1996 and 1997) are a reason for special concern, but it is impossible to determine whether such episodes now are more frequent than in the past.

It could be argued that mass deaths of suckers is a natural phenomenon caused by very high abundances of algae that have always been characteristic of Upper Klamath Lake. Or it could be argued, without particularly strong support, that mass mortality is more frequent or more severe than it used to be. It is not necessary, however, to resolve this point for ESA purposes. Because the abundances of the endangered suckers have been drastically reduced, any factor that leads to a larger population should be favored as a step toward recovery of the species, even if it involves a natural mortality mechanism. Thus, reducing mass mortality, whether natural or not, should be counted as beneficial to the welfare of the species and should be pursued.

Conditions commonly associated with fish kills include high temperature, intense blooms of bluegreen algae, high incidences of copepod (*Lernaea*) infestations (see Table 6-3), cysts, lesions, infection with *Flavobacterium columnare* (columnaris disease), high pH, high concentrations of unionized ammonia, and low concentrations of dissolved oxygen (Perkins et al. 2000b, Chapter 3). Before kills, some fish apparently move to the Link River (Gutermuth et al.

1998), and others (mainly redband trout) become concentrated in specific refuge areas, including Pelican Bay, Odessa Creek, and the Williamson River mouth. Refuges often contain springs that offer much better water quality than the lake itself (Bienz and Ziller 1987). Mortality of fish during routine sampling with trammel nets also increases during the weeks preceding a fish kill (USFWS 2002).

Although USFWS (2002) went to considerable lengths to examine the possible direct influence of high water levels in Upper Klamath Lake on sucker welfare, the data now on hand contradict the hypothesis that water level is associated with fish kills (NRC 2002, Figure 3; Chapter 3). Fish kills have occurred in years of low, average, and above-average median August lake levels. Water level may affect the accessibility of refuges that are reportedly used by large fish during periods of poor water quality and fish kills, but the data on this topic are largely anecdotal (see Buettner 1992 unpublished memo, USFWS 2002, Appendix C, and below).

High incidences of parasites, bacterial infections, and other anomalies imply that stressful conditions exist in Upper Klamath Lake for several weeks before the appearance of dead fish. Loftus (2001 cited in USFWS 2002) developed a "stress-day" index that accounts for multiple stress factors related to water quality. In 1990-1998, accumulated stress days were maximal in July and August during the fish-kill years of 1995 and 1997. The stress-day index approach is useful in that it involves regular, coordinated monitoring focused on water quality, meteorology, fish condition (parasite frequency, body condition, and so on), and attention to increased numbers of adults in the Link River or presumed refuges. When conditions and early warning signs converge, whatever remedial actions are feasible should be taken, possibly including oxygen supplementation at specific locales where suckers aggregate (Chapter 3).

In some lakes, mass mortality of fish occurs under ice ("winterkill"), usually in association with low concentrations of dissolved oxygen. Winterkill is not known to have occurred in Upper Klamath Lake or in any other lakes occupied by endangered suckers. Thus, the relevance of winterkill to Upper Klamath Lake remains hypothetical, as do management actions that would minimize its likelihood or effect.

Winter mortality (but not necessarily winterkill) has been postulated as the cause of a 90% reduction of first-year juvenile suckers in Upper Klamath Lake from late fall to early spring and population reductions in other species (Simon and Markle 2001). Comparable data are needed on winter mortality in surrounding water bodies with better water quality (such as Clear Lake) to determine whether the 90% mortality figure is extreme.

Concern over winterkill is justified, especially if water quality deteriorates further or if an exceptionally cold winter results in an unusually long period of ice cover. Improvement in water quality in the lake probably would reduce the likelihood of winterkill, but may be infeasible over the short term. Winter monitoring of oxygen should be undertaken in any event (Chapter 3).

Loss of Habitat

Adult Lost River suckers and shortnose suckers prefer open water; they use flowing waters chiefly for spawning. Total lake habitat available to suckers throughout the Klamath basin is a fraction of its original extent because of drainage and other water-management practices (Chapter 2). Even where it persists, habitat for adults may be compromised during late summer. Adult suckers appear to prefer water that is deep and turbid, and thus dark (USFWS 2002), but degraded water quality in summer apparently forces fish to use specific areas of shallow, clear water, such as the mouth of Pelican Bay in Upper Klamath Lake.

Factors Relevant to All Life-History Stages

A number of factors, some of which have already been mentioned, are potentially relevant to all life-history stages, although further research may show them to be more relevant to some stages than to others. Most prominent is poor water quality, which is linked not only to mass mortality of adults but potentially to undocumented mortality of other stages and to stress, which in turn may be a cause of anomalies, parasitism, and disease in multiple life-history stages. A second complex of factors that may apply broadly across stages, but still in unknown ways, falls under the heading of predation and competition, primarily from nonnative fishes. A final factor that cannot yet be attached to any particular life-history stage is hybridization, which may change populations genetically.

Water Quality

Suckers of Upper Klamath Lake suffer from high diversity and high incidence of deformities, parasites, lesions, cysts, and infections. The afflictions of adult suckers include eroded, deformed, and missing fins; lordosis; pughead; multiple water-mold infections; reddening of the fins and body due to hemorrhaging; cloudiness of the skin caused by low mucus production; loss of pigmentation; external parasitic infection by copepods and leeches; lamprey wounds; ulcers; gas emboli in the eyes; exophthalmia; cataracts; and a high incidence of gill, heart, and kidney abnormalities after fish kills. Plunkett and Snyder-Conn (2000) reported body-anomaly rates of 8-16% in larval and juvenile suckers. Juvenile suckers suffered infestation with copepods and trematodes of 0-7% in 1994-1996 and 9-40% in 1997-2000; shortnose suckers generally show higher rates of infestation than Lost River suckers (USFWS 2002 based on Carlson et al. 2002). Data on both species in Upper Klamath Lake and at river spawning sites also indicate relatively high frequencies of abnormalities in adults (Table 6-3). Spawning and nonspawning fish do not show substantial differences in the incidence of such indicators, except that copepod infestations appear to be higher in shortnose suckers and eye damage is higher in river-spawning fish of both species. The latter finding might reflect crowding of fish downstream of Chiloquin Dam or injuries to the fish as they attempted to negotiate the unsuitable fish ladder at the dam.

The widely used Index of Biotic Integrity (Karr et al. 1986) incorporates 1% as a threshold criterion for anomalies; sites with fish above this threshold receive the lowest metric scores for their ability to support a diverse biota. The appropriate threshold may vary geographically and by taxa, however. For the Willamette River, Hughes and Gammon (1987) identified 6% as a threshold. Hughes et al. (1998) proposed a more general threshold of 2%. Most collections from all size classes of Upper Klamath Lake suckers exceed these thresholds. It is not known why Clear Lake, with its better water quality and apparently stable population, also

Table 6-3. Incidence (%) of Various Indicators of Stress in Suckers of Upper Klamath Lake Based on Visual Inspection

	Incidence, %				
	Lampreys Wounds	Copepods Infections	Eye Damage	Emaciation	Wounds
Lost River Suckers, Live Fish, 2001					
Lake spawning	40	22	4	0	1
River spawning	48	28	22	0	2
Lake non-spawning	51	18	8	1	2
Shortnose Suckers, Live Fish, 2001					
Lake spawning	53	30	3	0	0
River spawning	38	51	16	0	1
Lake non-spawning	48	33	8	0	4
Fish Kill					
1997		73[a]			

[a] Based on Foott 1997 and Holt 1997 in USFWS 2002; incidence of *Columnaris* disease was 92% and 80%, respectively, during the 1996 and 1997 fish kills (USFWS 2002).
Sources: Coen et al. 2002, Cunningham et al. 2002, Hayes et al. 2002.

is characterized by "heavy parasite loads on suckers and other fish" (Snyder-Conn, personal communication cited in USFWS 2002, Appendix E, p. 38).

Even if infections and afflictions do not lead directly or even indirectly to death, they are likely to inhibit growth (e.g., M.R. Terwilliger et al., Oregon State University, Corvallis, Oregon, unpublished material, 2000) and reproduction and may compromise an individual's ability to resist other sources of stress. Without better baseline and reference values for suckers in other water bodies in and out of the Klamath basin, it is difficult to state categorically that the incidence of anomalies is extraordinary, but field researchers who work with fish seldom observe affliction rates approaching those found in Upper Klamath Lake.

Nonindigenous Species as Predators and Competitors

Eighteen of the 33 fish taxa in the upper Klamath basin are nonnative (Chapter 5). The nonnatives dominate numerically in many habitats and probably influence native species, including the endangered suckers, through predation and competition. Competition is particularly difficult to quantify in nature (Fausch 1988, 1998). Thus, it is not often possible to invoke competition as a major cause of problems in a population, and it also is difficult to moderate competition even where it can be demonstrated. In contrast, predation on native fishes by nonnative fishes is easily demonstrated; it can have devastating effects on native fishes (e.g., Fuller et al. 1999). In Upper Klamath Lake, introduced fathead minnows may prey on larval suckers, as shown in laboratory enclosures (Dunsmoor 1993, cf. Ruppert et al. 1993), although the applicability of the laboratory studies to conditions in nature is uncertain. Juvenile and adult yellow perch and juvenile largemouth bass consume larvae, as may Sacramento perch, most other centrarchid sunfishes, and the two bullhead species present in Upper Klamath Lake.

Juvenile and adult largemouth bass also could feed on juvenile suckers, although adult suckers reach a body size that provides them refuge from fish predators. Comparisons of Upper Klamath Lake with other lakes in this regard could be useful. With the exception of Sacramento perch, Clear Lake apparently has been spared significant introductions of nonnative fishes, and its populations appear to be stable. A species list for Gerber Reservoir is not readily available.

The presence of numerous and diverse nonnative fishes in the Klamath system complicates recovery efforts. Nonnative species typically do well in disturbed systems (Moyle and Leidy 1992). Given that attempts to reduce abundances of nonnative fishes usually are unsuccessful, the best tactics for decreasing the success of these invaders are to discourage future introductions (especially of predators), to restore water quality if possible, and to prevent movement of nonnative fishes within the basin. Selective control of nonnative species has been pursued in some environments (Ruzycki et al. 2003), however, and should not be ruled out entirely for Upper Klamath Lake.

Hybridization and Introgression

Hybridization results in wasted spawning and loss of genetic diversity through elimination of rare alleles. Introgression (backcrossing of hybrids with parental species) can eventually lead to the extirpation of a rare species, as apparently has happened to the endangered June sucker, *Chasmistes liorus liorus*, which hybridizes readily with the more abundant Utah sucker, *Catostomus ardens* (Echelle 1991). The original ESA listing document for Klamath suckers (53 Fed. Reg. 27130 [1988]) cited apparently high rates of hybridization among the three Upper Klamath Lake sucker species, especially between shortnose suckers and Klamath largescale suckers, and cited hybridization as a potential contributor to loss of genetic integrity and decline of species. Apparent hybrids, as indicated by morphological intermediacy, are commonly found in the Williamson River downstream of Chiloquin Dam and in sucker populations of Clear Lake, where crosses between Lost River suckers and Klamath largescale suckers are most frequently suspected (e.g., Cunningham et al. 2002; Moyle 2002; D. Markle, Oregon State University, Corvallis, Oregon, personal communication, 2002). Recent anatomical studies of hybridization, however, imply that it is a rare occurrence. Among spawning fish captured in Upper Klamath Lake in 2001, 0.2% of fish from shoreline spawning sites, 4% from the lower Williamson River, and 6% occupying the area below Chiloquin Dam were apparent hybrids (Cunningham et al. 2002, Hayes et al. 2002, Janney et al. 2002). In contrast, one-third of fish caught at Chiloquin Dam in 2000 appeared to be anatomically intermediate. Morphological studies may overestimate hybridization; allozyme frequency and nuclear genetic data indicate that recent hybridization is rare, that nominal species are all valid, and that little genetic divergence has occurred among populations within species (D. Buth, University of California at Los Angeles, Los Angeles, California, personal communication, 2002; Dowling 2000; T. Dowling, Arizona State University, Tempe, Arizona, personal communication, 2002). Microsatellite data indicate, however, that the three species present in the Lost River (largescale, shortnose, and Lost River suckers) are significantly different from suckers in Upper Klamath Lake and the upper Williamson River (G. Tranah, Harvard School of Public Health, Boston, Massachusetts, personal communication, 2002).

Overall, morphological data indicate that hybridization has occurred, but current genetic analyses reveal that Lost River suckers and shortnose suckers are distinct and that the identity of the species has not been eroded by extensive hybridization. High priority should be attached to further genetic analysis that will give more information on hybridization and on the genetic structure of currently isolated populations.

Before the Klamath Project was completed, all sucker habitats were subject to interchange of fish (Chapter 2). Dams and irrigation canals isolated populations to an extent that could ultimately affect the genetic diversity of the species. None of the primary dams in the Klamath basin allow passage of suckers. Efforts to protect the species with regard to range fragmentation should focus on habitat protection and improvement of all subpopulations and on construction of ladders of proven effectiveness or removal of barriers to improve exchange among subpopulations.

Other Issues Relevant to Recovery

Other Natives and the Paradox of Persistent Endemics

Shortnose and Lost River suckers apparently are more susceptible to degraded habitat conditions or other factors, such as predators, than any of the 14 other native species. Blue chub and tui chub do appear in some fish kills, sometimes in large numbers, but their populations remain large in Upper Klamath Lake, as do populations of Klamath Lake sculpins and redband trout. Even the Klamath largescale suckers in the upper Klamath basin and Klamath smallscale suckers in the lower basin seem not as affected by anthropogenic change as Lost River and shortnose suckers, although the Klamath largescale sucker is listed as a species of special concern in California (Moyle 2002). Introduced species, such as yellow perch and fathead minnow, appear to be unaffected by poor water quality. Sacramento perch, which have been greatly reduced throughout their native range (Moyle 2002), apparently are doing well in the Klamath basin. Explanations for the exceptional vulnerability of shortnose and Lost River suckers could be applied to recovery efforts.

One line of evidence is related to physiological tolerances among species, but this information is limited. Falter and Cech (1991) found that shortnose suckers were less tolerant of elevated pH than were Klamath tui chub and Klamath largescale suckers (Chapter 5). Additional comparative studies of physiological responses to water-quality degradation in the Klamath basin are needed. Overall, more and better information is needed on the biology and population status of nonsucker species in the upper basin (Chapter 5). Because all native Klamath fishes are endemics, any significant declines in their populations could trigger ESA actions. Although research efforts directed specifically at native fishes other than the listed suckers would be desirable, information on them can be collected in conjunction with studies of suckers. Some of the species can be used as indicators of water quality and habitat conditions and would provide insight into the welfare of the endangered suckers, especially where differences in physiological tolerance can be demonstrated. Comparisons between endangered Klamath suckers and other catostomid species in the Klamath basin and between Klamath suckers and lake suckers elsewhere could provide additional, invaluable insight into solutions to problems in the Klamath basin.

Captive Propagation

Captive propagation is a controversial means of protecting endangered species. Successful propagation can lead to complacency about the condition of natural populations and to delay in the correction of the original causes of decline, but it also can serve as insurance against catastrophes. Although Klamath suckers have not reached the point where captive propagation is necessary, many conservation practitioners recommend against waiting until there is no alternative to captive propagation, because by then genetic resources are diminished and problems with rearing methods may be disastrous.

The Klamath Tribe has established a sucker holding and rearing facility (the Klamath Tribes Native Fish Hatchery) at Braymill near Chiloquin. The facility has been used for physiological and behavioral studies and for fertilization and larva-rearing trials (e.g., Dunsmoor 1993; L. K. Dunsmoor, Klamath Tribes, Chiloquin, Oregon, personal communication, September 3, 2002). The facility could serve as the core of a captive-propagation effort if populations continue to decline. Methods already developed there can be used, perhaps with advice based on successful propagation of cui-ui at the David Koch Cui-ui Hatchery in Sutcliffe, Nevada, if captive propagation proves necessary.

Critical Habitat

Critical habitat, as defined by the ESA (Chapter 9), was not identified for the Klamath suckers at the time of original listing, and has yet to be completed for either endangered species, although a draft proposal appeared in 1994 (59 Fed. Reg. 61744 [1994]). On the basis of established ESA criteria (for example, water quantity and quality; physical habitat appropriate for spawning, rearing, and feeding; and protection from predation and climatic stress), USFWS identified six critical-habitat units (CHUs) in the basin: Clear Lake and its watershed, Tule Lake, the Klamath River, Upper Klamath Lake and its watershed, the Williamson and Sprague Rivers, and Gerber Reservoir and its watershed. All except Gerber Reservoir are habitat units for both sucker species; Gerber Reservoir contains only shortnose suckers, but Lost River suckers presumably could live there.

The draft critical-habitat determination (59 Fed. Reg. 61744 [1944]) and its recommendations should be reviewed and revised in light of recent findings. The process of identifying critical habitat for both species needs to receive higher priority and should be more specific. In designating Upper Klamath Lake a CHU, USFWS (59 Fed. Reg. 61744 [1994]) did not identify specific areas of particular value. The CHU approach could be expanded to include the needs of specific life-history stages, for example, east coast springs for spawning, Williamson River mouth and nearby shorelines as a nursery region, Modoc Point and Goose Bay as staging areas before spawning, and west coast bays as postspawning aggregation areas (see Chapter 5). Buettner (1992) identified sites that have the greatest potential as adult refuges at low lake levels on the basis of their size, proximity to the main lake, relative water quality, and density of submerged vegetation. The issue of water-quality refuges needs more study relative to critical habitat. If the postulated patterns can be verified and the location and use of these apparent water-quality refuges can be confirmed, they might be designated as critical habitat and considered for special protection.

Although there is only weak pressure for development in the Klamath basin, the human population of the area has grown, and future growth is likely (Chapter 2). Proposals for new construction or use of the lake should take into account possible adverse effects on suckers. For example, an article in *SAIL* magazine for July 2002 identified Howard Bay, Pelican Bay, and Harriman Springs as desirable destinations for boaters. Howard Bay apparently is a preferred aggregation area for postspawning shortnose suckers (Coen et al. 2002); Pelican Bay was identified by Buettner (1992) as a refuge for suckers during the fish kills of July 1971 and August 1986 and was considered the best sucker refuge site on the west shoreline when lake levels drop; and Harriman Springs is a former spawning site. Increased boat traffic, development, groundwater pumping, or other activities may adversely affect these sites.

LESSONS FROM COMPARATIVE BIOLOGY OF SUCKERS

Of the 63 species of suckers in the world, 61 are endemic to North America. Among the few known extinctions of freshwater fishes in North America, suckers figure prominently. Previously abundant, sometimes widespread species have disappeared, including the harelip sucker (*Lagochila lacera*) and the Snake River sucker (*Chasmistes muriei*). Fully 35% of sucker species are imperiled (Warren and Burr 1994), and eight have federal endangered or threatened status (50 CFR 17.11 [1999]).

Populations of large suckers in general and lake suckers in particular have declined largely because of anthropogenic factors. Although there is an obvious need for concern about these very American fishes, comparative data indicate that they can survive long periods of interrupted recruitment and can recover from these remarkable hiatuses in reproduction if factors causing decline are reduced. For example, decline has occurred in other lake suckers: cui-ui experienced no known recruitment from 1950 to 1969; June suckers had experienced at least 15 yrs without recruitment by the middle 1980s, and that probably continued into the 1990s; some populations of razorback suckers (*Xyrauchen texanus*) experienced 20-30 yr without recruitment; and Utah suckers (*Catostomus ardens*) did not reproduce successfully between the middle 1960s and the early 1990s.

Despite extended interruptions in breeding, several species of suckers have responded successfully to recovery programs. Cui-ui successfully spawn in the Truckee River because of enhanced flows and are propagated in a hatchery managed by the Paiute Tribe, from which they are regularly transplanted into Pyramid Lake, where they are abundant (USFWS 1992b). Efforts to promote recovery of June suckers have been under way since the early 1990s and appear to have been successful; they include water-allocation agreements, refuge-population establishment, and captive breeding and release (USGS 1998). The robust redhorse, *Moxostoma robustum*, a large sucker thought to have undergone population declines in Atlantic slope drainages, is now propagated and planted and has shown successful recaptures in three southeastern rivers (Jennings et al. 1998; C. Jennings, U. S. Geological Survey, Athens, Georgia, personal communication, 2002). An extensive recovery program for razorback suckers instituted in 1988 includes captive rearing and transplantation, habitat acquisition and protection, and control of nonindigenous species; success has been mixed (Minckley et al. 1991, Mueller and Marsh 1995). This general picture of decline, public concern, multifaceted efforts at recovery, and evidence of success can suggest actions that might be successful with the Klamath basin sucker species.

All four living lake suckers (shortnose sucker, Lost River sucker, cui-ui, and June) are relatively large and long-lived (Chapter 5). High tolerance of poor water quality implies that the fishes evolved in habitats that periodically experience extremes of water quality. Long life in these suckers may reflect an evolutionary history that included harsh conditions that often resulted in reproductive failure, perhaps for many consecutive years. Exceptional longevity is a cause for optimism in that it allows the fish to recover from population declines once conditions favorable to survival are restored (Scoppettone and Vinyard 1991).

Age distributions in Upper Klamath Lake suckers, as reflected in the fish-kill data, show apparent resilience in Klamath species (e.g., Cooperman and Markle 2003). Heavy fishing pressure resulted in low numbers of old suckers until 1987, when the fishery was eliminated. Numbers of adults later increased sharply (Figure 5-4). The rapid increase demonstrates the positive effect of closing the fishery. More important, the increase shows that even after prolonged population declines brought about by overfishing, a relatively small number of large, highly fecund individuals can produce many young and help to restore a population (Cooperman and Markle 2003). Even slight improvements in conditions favorable to suckers in Upper Klamath Lake, its tributaries, and surrounding water bodies could contribute to recovery.

CONCLUSIONS

Despite elimination of fishing for the shortnose and Lost River suckers in 1987, these two listed species have failed to show an increase in overall abundance. Apparently stable populations with regular recruitment and the presence of all life-history stages at appropriate abundance are found only in Clear Lake and Gerber Reservoir. Thus, the listed suckers at these two locations require special degrees of protection, both in the lakes themselves and in tributary waters where the suckers spawn.

The two listed suckers are present in Upper Klamath Lake, where they reproduce and show the full spectrum of age classes indicating successful maturation of at least some individuals. This population has not increased in abundance, however, because of episodes of mass mortality affecting large fish and possibly other factors as well. Populations at other locations (the mainstem reservoirs, the main stem of the Lost River, and Tule Lake) are of very low abundance and consist primarily of adults; no full representation of age classes is present at these locations. Suckers have been eliminated entirely from the middle portion of the main stem of the Lost River, from Lower Klamath Lake, and from Lake of the Woods.

Small irrigation dams and the larger Chiloquin Dam across the main stem of the Sprague River impede the movement of suckers attempting to spawn in the tributaries to Upper Klamath Lake. Elimination of Chiloquin Dam could greatly expand any potential spawning area, although channel and riparian improvements to the upper Sprague might be necessary to achieve the full benefit of dam removal.

Spawning of suckers in tributaries to Upper Klamath Lake is successful in producing fry, but the spawning areas do not receive special protection and are poorly studied. Physical restoration of tributary spawning areas is a matter of high priority and will involve exclusion of livestock and other measures designed to promote conditions that favor spawning of the suckers. Physical restoration near the mouth of the Williamson River as it enters Upper Klamath Lake is also important.

Water level in Upper Klamath Lake shows no relationship to water-quality conditions that result in mass mortality of adult suckers or other potentially adverse water-quality conditions. In addition, water level shows no relationship to year-class strength or to abundance of fry or juveniles over the years during which standardized sampling is available. Thus, maintenance of water levels above recent historical levels in order to increase the abundance of suckers by maximizing the area of habitat where young suckers are found is not supported by the currently available evidence. Water levels lower than recent historical levels could have undocumented adverse effects and therefore are inadvisable. Experimental maintenance of specific water levels could be incorporated into a management plan, however, through agreements between USFWS and USBR, if USFWS sees merit in further studies of water-level control.

The two listed suckers spawn in specific lakeside areas of Upper Klamath Lake, typically in association with the presence of springs. Some spawning areas have been abandoned entirely, possibly because of the elimination, through fishing, of specific groups of fish that habitually used these areas. Some spawning areas show signs of anthropogenic degradation. Selective restoration of these areas and manipulation of stocks to encourage bonding of specific groups of suckers to the unused sites could be beneficial in spreading the reproductive risk of the sucker populations.

Suckers of all ages in Upper Klamath Lake historically have been entrained into the A Canal, which is the main supply conduit for USBR's Klamath Project. Screening of this source of mortality is scheduled for summer of 2003, but it cannot be expected to prevent mortality of very small fish. Refinement of the operation of the screens as recommended by USFWS (2002) might reduce the mortality of very young fish. The Link River Dam intake units remain unscreened, and thus remain a source of mortality for fish of all ages.

Suckers of Upper Klamath Lake and at other locations where suckers are present in the upper basins share their habitat to varying degrees with nonindigenous species, some of which are known to prey upon or compete with young suckers. Elimination of nonindigenous species over very large systems such as Upper Klamath Lake is beyond the current state of the art, but programs designed to prevent additional introductions and prevent the spread of presently nonindigenous species would be highly advisable. Because the actual effect of the nonindigenous species on the suckers is poorly known, it is difficult to judge the importance of this factor based on current information.

Hybridization among sucker species was an original concern of considerable importance to the listing of the suckers. Subsequent studies have reduced the level of this concern, but it would be advisable to have more information on the genetic identities of suckers at various locations in the upper basin.

Captive propagation is a possibility and could be conducted on a pattern that has been developed for populations of related suckers at other locations. Captive propagation is probably disadvantageous at present, however, in that it tends to undermine incentives for return of the populations to a self-sustaining basis, which may still be possible in the Klamath basin. Continued decline of the population sizes or loss of any major subpopulations would indicate a need for captive propagation.

The long life history of suckers requires extended observation as a means of judging population trends. Benefits of restoration actions will not necessarily be evident until the fish benefiting from these actions have achieved spawning capability. Similarly, the negative effects of mortality focused on large fish may become evident only gradually, but could extinguish entire subpopulations.